Ecology of the Arrow Squid (*Nototodarus gouldi*) in Southeastern Australian Waters.

A Multi-Scale Investigation of Spatial and Temporal Variability.

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Declaration of Originality

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This project was approved by the University of Tasmania Animal Ethics Committee (Permit A0006997, 9/10/2002).

Statement of co-authorship

One chapter of this thesis (chapter 5) has already been published in a peer reviewed journal:

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Jeremy Lyle provided logistical support for the project and assisted with the refinement and presentation of the research paper.

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Abstract

Phenotypic plasticity together with a short lifespan, rapid growth and the ability to move over considerable distances mean that squid populations are extremely responsive to changing environmental conditions, and this generates highly variable and complex patterns of population ecology. This study examined the population ecology of the ommastrephid squid *Nototodarus gouldi* in southern Australian waters; investigating how patterns of distribution and abundance vary in space and time, and the factors that may be driving these patterns.

Broad scale GIS and statistical (GAM and GLM) analyses of trawl fishery observer data identified clear 'hotspots' of *N. gouldi* abundance in southeastern Australian waters, which corresponded with areas of significant mesoscale oceanographic activity (i.e. strong shelf break fronts, convergence zones and upwelling). Abundance was seasonal, but this seasonality varied between locations. Remotely sensed sea surface temperature and chlorophyll-a concentration were unable to account for the spatio-temporal patterns in *N. gouldi* encounter and catch rates, possibly due to a temporal mismatch between local oceanographic activity and the evidence of its effect on *N. gouldi*.

Lagged relationships between local environmental conditions and *N. gouldi* abundance were then examined on an annual scale for one region- the Bonney Coast, a 'hotspot' area subject to seasonal upwelling activity. Local wind speed and ENSO were both strongly correlated with annual abundance, most likely due to their influence on mixing and upwelling activity, and thus prey availability. Cross validation of a linear model incorporating these environmental variables suggested reasonably good predictive ability. A negative correlation between jig and trawl derived indices of abundance however suggests that inter-annual variability is driven by distributional changes as well as recruitment variability, with the depth distribution of *N. gouldi* possibly changing in response to the position of the upwelling front.

Population structure and life history characteristics of *N. gouldi* on an inshore jig ground in southeastern Tasmania exhibited significant variability over four years, although patterns were not always consistent for the two sexes, particularly in relative levels of reproductive investment. Abundance was also highly variable over this four year period however there was no clear relationship between biological characteristics and available abundance. Squid in a year of extremely high abundance were a similar size and age to those sampled in years of low abundance; the change in biomass therefore attributed to changes in numbers of squid.

Nototodarus gouldi appear to undertake ontogenetic bathymetric migrations, with squid recruiting to the jig fishery as small juveniles, growing and maturing over the summer before moving away, most likely into deeper waters where large mature individuals are caught by trawlers. A change in sex ratio over the jig season also indicates that males may leave the jig grounds earlier than females. Tracking of *N. gouldi* using an automated acoustic telemetry array also showed that squid moved away from the inshore jig grounds, but this movement was not in any way synchronous, with individuals apparently leaving over an extended time period in the

season of the tracking study- a year of very low abundance. In contrast, the persistence of large mature *N. gouldi* on the jig ground when abundance was extremely high suggests the increased numbers of squid may be due to longer residency times and the accumulation of individuals.

Thus, the ecology of *N. gouldi*, like many other commercially exploited ommastrephid squid, appears to be closely linked to hydrography and ocean productivity. They are in greatest abundance where the shelf break is strongly defined or where other mesoscale oceanographic activity is present (e.g. upwelling), and variability in biomass cycles also appears to be related to the seasonality and nature of local mesoscale oceanography. Further investigations are needed to elucidate the finer-scale variability and detail of the mechanisms driving these patterns. In particular, investigation into the linkages between populations on jig and trawl fishery grounds and the relationship between ontogeny and depth distribution appear to be critical for understanding patterns of distribution and abundance, and for the development of appropriate fishery assessment models.

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Chapter 1:

General Introduction

Life Cycles and Population Ecology of Squid

Although squid generally fill a similar ecological niche to teleost fish, their physiology and life cycle characteristics set them well apart, specifically their short lifespan, rapid growth and development, and phenotypic plasticity (Boyle & Boletzky 1996). Most squid species live for only a year or less (Jackson & O'Dor 2001) and thus the population is made up of new individuals each year. Squid growth is much faster than in similar sized teleost fish (Forsythe & Van Heukelem 1987, Lee 1994), and unlike fish, they do not reach an asymptotic size (Alford & Jackson 1993). This is evident at the cellular level, with squid growing over their entire lifespan by both hypertrophy (increased muscle size) and hyperplasia (addition of new muscle fibres, Moltschaniwskyj 1994, Pecl & Moltschaniwskyj 1999), while teleost fish generally cease hyperplasia with age (Jackson & O'Dor 2001). Squid have exceptionally high growth efficiency, with a protein-based metabolism that rapidly converts energy into growth rather than storage (O'Dor & Webber 1986, Lee 1994, Moltschaniwskyj & Semmens 2000). The metabolic and growth rates of squid are indeed higher than many poikilothermic vertebrates, including most teleost fish, and can in fact be as high as some mammals (Pörtner & Zielinski 1998, Zielinski & Pörtner 2000).

Although genetic variation is relatively low in squid populations, they show a high degree of phenotypic plasticity in all life history characteristics (Boyle & Boletzky 1996). Large intra-specific variability has been documented for egg size and rates of embryonic development (e.g. Steer et al. 2002, Steer et al. 2003a), hatchling size (e.g. Ikeda et al. 1999, Steer et al. 2003b, Pecl et al. 2004a), growth (e.g. Arkhipkin 1996, Pecl 2004, Jackson et al. 2005), age and size at maturity (e.g. Arkhipkin & Laptikhovsky 1994, Boyle et al. 1995, Jackson & Yeatman 1996, Arkhipkin et al. 2000) and reproductive investment (e.g. Pecl 2001, McGrath Steer & Jackson 2004, Smith et al. 2005). Phenotypic plasticity together with a short lifespan and rapid growth mean that squid at the individual, and ultimately population level are extremely responsive to changing environmental conditions. Coupled with the ability to move over considerable distances, these features contribute to the unpredictable and complex patterns of distribution and abundance evident for many squid species (Boyle & Boletzky 1996). Large seasonal, inter-annual and spatial variability in abundance are therefore characteristic features of most squid populations.

Although ageing studies show that many species spawn and hatch year-round (e.g. Arkhipkin et al. 2000, Jackson et al. 2005), biomass production is typically seasonal, with peaks on an annual or bi-annual scale. This may be due to differential survival and growth under seasonally changing environmental conditions, particularly during the early life history stages (O'Dor 1998, Grist & des Clers 1999). Squid hatched in different seasons can have very different biological characteristics (e.g. Jackson 1995, Dawe & Beck 1997, Arkhipkin et al. 2000, Jackson & Moltschaniwskyj 2001b, Pecl & Moltschaniwskyj 2006) and laboratory based experimental studies

have confirmed the importance of both temperature and food availability to rates of growth (Forsythe 1993, Forsythe et al. 2001, Jackson & Moltschaniwskyj 2001a). Later hatched cohorts can grow faster and 'catch-up' with the earlier hatched cohorts when exposed to better conditions during the important juvenile stages (e.g. Hatfield et al. 2001, Pecl 2004), ultimately influencing the seasonal timing and relative size of the biomass recruiting to the population (Grist & des Clers 1998, 1999, Reiss et al. 2004).

Without the stability of multiple year classes that longer lived fish populations possess, population size can also vary dramatically from year to year, sometimes by several orders of magnitude (Rodhouse 2001). Annual recruitment is strongly influenced by environmental variability, particularly at the time of hatching (Bakun & Csirke 1998), and environment-recruitment relationships have been described for a wide variety of commercially exploited species including *Illex argentinus* on the Patagonian shelf (Waluda et al. 1999, Waluda et al. 2001a), *I. illecebrosus* in the western Atlantic (Coelho & Rosenberg 1984, Dawe & Warren 1993, Dawe et al. 2000), *Todarodes pacificus* and *Thyanoteuthis rhombus* in the Sea of Japan (Sakurai et al. 2000, Kang et al. 2002, Miyahara et al. 2005), *Dosidicus gigas* in the eastern Pacific (Waluda et al. 2004, Waluda & Rodhouse 2006), *Loligo forbesi* and *L. vulgaris* in the English Channel and North Sea (Robin & Denis 1999, Pierce & Boyle 2003), and *L. gahi* in the southwest Atlantic (Agnew et al. 2000).

The mechanisms by which the environment may control temporal variability in recruitment are however, not always clear. The environmental variables most often examined are those which are most readily available, usually sea surface temperature (SST) and climatic indices such as the North Atlantic or Southern oscillation indices (NAO and SOI). While SST can exert a direct effect on embryonic development (Villanueva 2000a, Boyle et al. 2001, Villanueva et al. 2007) and post-hatching growth rates (Forsythe 1993, 2004), it may also act as a proxy for the productivity of the system or mesoscale dynamics such as the position of a current important for dispersal or prey concentration (e.g. Jackson & Domeier 2003, Roberts 2005, Waluda & Rodhouse 2006). Climatic indices most likely reflect the influence of broad-scale atmospheric circulation patterns on the oceanographic regime (e.g. Dawe et al. 2000, Dawe et al. 2007).

The nature of squid life cycles and their ability to respond rapidly and dramatically to environmental change thus promote considerable temporal variability in abundance, at both seasonal and annual scales. Life history characteristics and population structure have also been shown to vary significantly over geographic scales. For example, Moreno et al. (2005) found that *L. vulgaris* in the eastern Atlantic and Mediterranean varied between locations in mean and maximum length and weight, condition (weight-at-length), size-at-maturity, levels of reproductive investment and the seasonal timing of spawning and recruitment. These differences were attributed to latitudinal changes in temperature, as well as the timing of productivity cycles related to upwelling activity. *Illex coindetti* sampled in several locations in the European Atlantic and Mediterranean (Arvanitidis et al. 2002) and northwest Africa (Arkhipkin 1996) also varied between locations in size-at-recruitment, timing of recruitment, condition, growth rate, maximum size and age, size-at-maturity and maturity structure. Some of these biological indices were correlated with SST and/or chlorophyll-a concentration (Arvanitidis et al. 2002). The timing and magnitude of

squid biomass cycles may therefore also vary between locations in response to the specific local environmental conditions encountered.

Spatio-temporal patterns of biomass for many squid species are further complicated by ontogenetic migrations. Many ommastrephid species, particularly those associated with high energy western boundary current systems (O'Dor & Coelho 1993), undertake large scale migrations between spawning and feeding grounds, often over thousands of kilometres (e.g. *I. argentinus*, Haimovici et al. 1998; *I. illecebrosus*, O'Dor & Dawe 1998; *T. pacificus*, Takami & Suzu-Uchi 1993, Mokrin et al. 2002; *Ommastrephes bartramii*, Bower & Ichii 2005). Loliginid squid undertake smaller scale movements (in the order of a few hundred kilometres or less), usually between feeding grounds in deeper waters and inshore shelf waters where they form dense breeding aggregations (e.g. *L. gahi*, Hatfield et al 1990, Hatfield & Rodhouse 1994; *L. vulgaris reynaudii*, Sauer et al. 2000; *L. forbesi* and *L. vulgaris*, Waluda & Pierce 1998, Sims et al. 2001). These movements, coupled to the timing of the life cycle, dictate the seasonal location of biomass (Boyle & Boletzky 1996), and may vary in timing and nature depending on the local oceanography and environmental conditions. For example, *L. forbesi* in the English Channel migrate earlier in warmer years (Sims et al. 2001), perhaps in relation to precocious maturation (Pierce et al. 2005).

Squid may also display environmental preferences, influencing how the biomass is spatially distributed. For instance the distribution of *I. argentinus* in the southwest Atlantic has been linked to sea surface and bottom temperature and the presence of thermal gradients (Waluda et al. 2001b, Bazzino et al. 2005, Sacau et al. 2005), and for *Loligo* spp. in the North Sea and English Channel a suite of variables including water temperature, salinity, sea level pressure, solar flux and wind direction may be important (Pierce et al. 1998, Waluda & Pierce 1998, Bellido et al. 2001, Denis et al. 2002). Environmental change can influence patterns of distribution and abundance, with range expansions and contractions evident in response to changing SST (e.g. Chen et al. 2006, Zeidberg & Robison 2007). As with recruitment models, the environmental relationships may be indirect in nature, instead reflecting mesoscale activity and/or prey availability (e.g. Ichii et al. 2002), the distribution of different water masses (e.g. Mokrin et al. 2002, Arkhipkin et al. 2004a), or may correlate with a decline in predators (Zeidberg & Robison 2007).

The short lifespan, rapid growth and development, high levels of phenotypic plasticity and mobility of squid all contribute to complex patterns of population ecology. They allow squid to act as ecological opportunists, responding rapidly and dramatically to environmental change, and this has led to terrestrial analogies of desert locusts (Rodhouse 2001) and weeds (O'Dor 1998). However these characteristic features of squid also grossly “exaggerate the difficulties of establishing useful generalizations about populations” (Boyle & Boletzky 1996, p985). Population abundance fluctuates greatly in space and time and this makes the quantification of the role of squid as predators and prey in ecosystem studies and the development of useful assessment and management strategies for commercially exploited stocks extremely difficult.

Traditional stock assessment techniques developed for longer lived fish populations are not relevant to squid, severely limiting the options available for fishery

assessment and management. Understanding the role of squid in the ecosystem is also complicated by their spatio-temporal variability in abundance, although they are clearly an important source of prey to higher predators. The availability of squid can influence the breeding success (Xavier et al. 2003) and distribution patterns (Jaquet & Gendron 2002) of higher predators, and may have a substantial influence on rates of natural mortality and recruitment of prey populations, including many commercially exploited fish (eg. Ivanovic & Brunetti 1994, Boyle & Rodhouse 2005).

This study examines the population ecology of the arrow squid, *Nototodarus gouldi* in southern Australian waters; describing patterns of distribution and abundance and investigating the factors shaping these patterns. Commercial fishing statistics and surveys of *N. gouldi* (JAMARC 1978a, 1978b, 1979, Willcox et al. 2001, Lynch 2004) suggest highly variable spatial and temporal trends in abundance, and while recent investigations have shed light on the life cycle of *N. gouldi* and spatial and seasonal trends in its growth and reproductive strategies (Jackson et al. 2003, McGrath Steer & Jackson 2004, McGrath-Steer 2004, Jackson et al. 2005), little is understood of its ecology, specifically patterns of distribution and abundance. *Nototodarus gouldi* is a key component of the southern Australian continental shelf and slope ecosystem, and spatial and temporal variability in availability may have considerable impacts on both predator and prey populations. *Nototodarus gouldi* also support the largest commercial cephalopod fishery in Australian waters, although industry development and management have been hindered by a lack of understanding of patterns of distribution and abundance.

Review of the biology, ecology and fisheries of *Nototodarus gouldi*

The Indo-Pacific arrow squid genus *Nototodarus* has three species- *N. sloanii* (Gray, 1849) occurring around southern New Zealand; *N. hawaiiensis* (Berry, 1912) broadly distributed in the tropical Indo-Pacific; and *N. gouldi* (McCoy, 1888), the study species, present around northern New Zealand and southern Australia (Dunning & Förch 1998). In Australian waters the distribution of *N. gouldi* ranges from southern Queensland on the east coast and mid Western Australia on the west coast, encompassing all southern coastal waters, including Tasmania (Dunning 1998, Dunning & Förch 1998).

Life Cycle

Nototodarus gouldi appear to live for up to 12 months, with sampled squid having maximum ages of 360 days for females and 325 days for males (Jackson et al. 2005). Female *N. gouldi* are consistently larger in size, reaching a maximum of 393 mm dorsal mantle length (ML) and 1655 g total body weight (BW), while the largest males recorded are only 366 mm ML and 1057 g (Jackson et al. 2003). Mature males have been observed from around 200 mm ML, with most males greater than 280 mm ML fully mature (O'Sullivan & Cullen 1983). Females attain sexual maturity at larger sizes than males, from around 280 mm ML, with most females mature at mantle lengths greater than 320 mm (O'Sullivan & Cullen 1983, Willcox et al 2001). These sizes at maturity are similar to those found for the species in New Zealand waters, where mantle length was shown to be a better determinant of maturity than age (Uozumi 1998).

Ageing studies suggest that *N. gouldi* have a protracted spawning period with hatching taking place throughout the year (Uozumi 1998, Jackson et al. 2005). They appear to be multiple spawners with eggs released in small batches (McGrath & Jackson 2002). Females are mated before they are fully mature and sperm is stored in buccal pouches around the mouth (McGrath & Jackson 2002). Eggs are fertilised as they pass the buccal mass and are transferred to a large pelagic egg 'balloon' (O'Shea et al. 2004). The egg mass is a free floating gelatinous sphere of at least 1.5m in diameter and contains several thousand eggs (O'Shea et al. 2004).

Population ecology

Allozyme electrophoresis on samples of *N. gouldi* collected from 6 locations around southern Australia revealed no evidence of more than a single species (Triantafillos et al. 2004). Allele frequencies were similar for all sites (separated by up to 4300 km) and all polymorphic loci, however the study was somewhat limited by small sample sizes low numbers of genetic markers and alleles per marker. The possibility of some population sub-structuring on the east coast of Australia was suggested and further molecular investigation using microsatellite analysis and/or mitochondrial DNA sequence data are needed to clarify any fine-scale variability in population structure.

Large-scale ontogenetic migrations of many commercially exploited ommastrephid squid are well documented (e.g. *Todarodes pacificus*, Takami & Suzu-Uchi 1993, Mokrin et al. 2002; *I. illecebrosus*, O'Dor & Dawe 1998; *I. argentinus*, Haimovici et al. 1998). However, tag-recapture studies off southeastern Australia (Machida 1983) and western New Zealand (Sato 1985), and studies of population biology (Uozumi 1998, Jackson et al 2005) provide no evidence of any similar migration by *N. gouldi*. Mature male and female *N. gouldi* have been found at all sampled locations in Australian waters, suggesting that spawning occurs across their entire range (Jackson et al. 2003, Jackson et al. 2005). *Nototodarus gouldi* paralarvae close to the probable size at hatching (0.8 to 1.0 mm ML) have also been collected over a broad area of the Australian continental shelf from southern Queensland to the western Great Australian Bight (Dunning 1985, Dunning & Förch 1998). Spawning in northern New Zealand waters also appears to occur across the entire geographic range of *N. gouldi* (Uozumi 1998).

Size and age structure of *N. gouldi* is complex and highly variable in space and time (Jackson et al. 2005). There is often a mix of several modal groups (Harrison 1979, Machida 1983, O'Sullivan & Cullen 1983), and hatch frequencies from monthly samples off western Victoria suggest up to four main cohorts within a year (Jackson et al 2003). The southern NSW population appears unique from those sampled elsewhere in Australian waters, with individuals being generally smaller for a given age, and maturing earlier (Winstanley et al. 1983, Jackson et al. 2003).

Little is known of patterns of distribution and abundance except from fishery statistics. *Nototodarus gouldi* is available year round to demersal trawlers fishing in shelf and slope waters and also appear seasonally in shallow coastal waters, where they are targeted by commercial jig fisheries (Winstanley *et al.* 1983, Willcox et al 2001). However the jig fisheries are highly localised and seasonal in nature and both catches and catch rates fluctuate greatly between locations and years. The timing of

availability on jig grounds also varies between different locations (Willcox et al. 2001, Lynch 2004, Sahlqvist 2007). Japanese surveys of *N. gouldi* in the 1970s and 1980s covered a much broader area of the shelf than the current jig fisheries, and also found a high level of spatial and temporal variability in availability (JAMARC 1978a, 1978b, 1979). It is not known what drives the variability in abundance of *N. gouldi*, but it is most likely related to oceanographic conditions and prey abundance given that these are important drivers of the distribution and abundance of other ommastrephid squid (Anderson & Rodhouse 2001). Growth rates are also highly variable among locations and seasons, and for female *N. gouldi*, correlated with ocean productivity (Jackson et al. 2003).

Prey & Predators

Stomach contents analyses have shown the diet of *N. gouldi* to consist of small planktonic crustaceans, fish and squids (Machida 1983, O'Sullivan & Cullen 1983, Smith 1983, Uozumi 1998). The relative contribution of crustaceans to the diet was negatively correlated with squid size, while the occurrence of cephalopod prey increased with size (O'Sullivan & Cullen 1983, Uozumi 1998). The fish component of the diet remained constant over all sizes of *N. gouldi* in one study (O'Sullivan & Cullen 1983), but increased in another (Uozumi 1998). The proportion of *N. gouldi* with empty stomachs also increased with size and maturity of both male and female squid (O'Sullivan & Cullen 1983, Uozumi 1998).

In southern Australian samples, pilchards (*Sardinops pilchardus*) and juvenile barracouta (*Leionura atun*) were the most common fish species identified in the diet of *N. gouldi* (Machida 1983, O'Sullivan & Cullen 1983). Crustaceans included *Leptochela sydeniensis* (a carid prawn), *Cirolana* sp. (an isopod), and other unidentified crabs (adults and megalopa larvae), isopods and amphipods. The cephalopod component of the diet was mostly ommastrephid squid and a few unidentified Octopuses. The majority of the squid prey appeared to be conspecifics of considerably smaller size than the predators, and this could not be attributed to post-capture cannibalism (O'Sullivan & Cullen 1983).

Stomach fullness of *N. gouldi* is greatest at night and dawn, and lowest at dusk (O'Sullivan & Cullen 1983, Uozumi 1998), suggesting that *N. gouldi* feed primarily at night. This is consistent with *N. gouldi* behaviour determined from an echo sounding and sonar study in which squid aggregated on the bottom during the day and then dispersed throughout the water column at night (Evans 1986). Jig fishing catch rates are also highest at night (Nowara & Walker 1998), although this is probably related to the use of lights as attractants. Vertical stratification of *N. gouldi* has been suggested, with smaller squid apparently feeding higher in the water column than larger squid (Nowara and Walker 1998), perhaps in response to prey distributions.

Nototodarus gouldi is a key prey species in southern Australia and is consumed in large numbers by many fish (Dunning et al. 1993, Young et al. 1997, Lansdell & Young 2007), birds (Hedd & Gales 2001) and marine mammals (Gales et al. 1993). The contribution of *N. gouldi* to the diet of these higher predators has been found to vary spatially, seasonally and inter-annually. For example, *N. gouldi* was more abundant in east coast swordfish (*Xiphias gladius*) and yellow-fin tuna (*Thunnus*

albacares) diets in winter compared to summer (Lansdell & Young 2007). In southern Australian waters however, Australian and New Zealand fur seals (*Arctocephalus pusillus doriferus* and *A. fosteri*) consumed relatively more *N. gouldi* during summer and autumn months (Gales et al. 1993, Page et al. 2005), although Littnan et al. (2007) found that such seasonal trends also varied between locations and years. Considerable inter-annual variability was also evident in the contribution of *N. gouldi* to the diet of Shy Albatross (*Thalassarche cauta*) during their breeding season off northwestern Tasmania (Hedd & Gales 2001). These spatial, seasonal and inter-annual patterns in the consumption of *N. gouldi* probably reflect the highly variable patterns of *N. gouldi* abundance as well as the foraging behaviour and preferences of the predators.

Commercial Fishery for N. gouldi in Australian waters

The commercial potential of squid resources in Australian waters was first recognised by the Japanese with the Golin Gyukuyo Fishing Company conducting surveys around Tasmania in 1969/70. Several feasibility surveys were then conducted by the Tasmanian Fisheries Division (Harrison 1979, Willcox et al. 2001) and the Japanese Marine Fishery Resources Research Centre (JAMARC 1978a, 1978b, 1979) during the 1970s and 80s. Commercial Japanese, Taiwanese and Korean squid jig vessels also fished Australian waters from 1977 to 1988 under joint venture partnerships with Australian companies, taking up to 8000 tonnes of *N. gouldi* each year from Tasmanian, Victorian and South Australian waters (Sahlqvist 2007). Domestic vessels first geared up for jig fishing in Tasmanian waters in 1972. However, interest levels quickly waned due to variable availability of squid, poor prices and limited market opportunities (Willcox et al. 2001).

The domestic jig fishery in Bass Strait began with just one vessel fishing in the 1986/87 season. Participation and annual catches through the early 1990s were low (a maximum of 17 vessels and 400 tonnes), primarily due to the seasonal and unpredictable availability of squid and relatively high running costs of light-equipped jig vessels (Sahlqvist 2007). A successful season in 1995 (over 1200 tonne) however, rekindled interest in the fishery and up to 40 vessels fished Bass Strait and western Victorian waters in the following two seasons. During the early and mid 1990s there was also small-scale jig fishing in Tasmanian State waters, with up to 17 local operators using hand-lines (Willcox et al. 2001). Following on from the expansion of the Bass Strait fishery in the mid 1990s, there was a rapid increase in the number of vessels fishing in Tasmanian State waters in 1998/99, with the entry of several new jig boats as well as boats usually based on the mainland. Participation in the jig fisheries has however, generally declined since the late 1990s, with less than 30 vessels active since 2000 (Sahlqvist 2007). This is due to the unpredictable nature of the fishery coupled with poor market prices and increasing competition with imported squid product.

All jig fishing for *N. gouldi* is conducted in shallow continental shelf waters, usually less than 150 m depth. There is little by-catch with less than 1% of the catch made up of squid species other than *N. gouldi* (most often *Todarodes filippovae* or *Ommastrephes bartramii*; Sahlqvist 2007). Very little effort is directed outside of the traditional fishing grounds off western Victoria, in Bass Strait and to a lesser degree southeast Tasmania, although reasonable catches are also taken occasionally from

waters off eastern Victoria (Willcox et al. 2001, Lynch 2004, Sahlqvist 2007). This concentration of effort over small discrete areas is unrelated to management restrictions, with the boundaries of the Commonwealth managed fishery (the Southern Squid Jig Fishery, SSJF) extending from southern Queensland (24°30'S) to the South Australian border with Western Australia (129°E), including Tasmanian waters beyond the 3 nautical mile State boundary. The Tasmanian State managed jig fishery has access to all Tasmanian waters within 3 nautical miles from the coastline.

The jig fisheries are highly seasonal with the majority of fishing occurring during the autumn months (February to June) in Bass Strait and western Victoria, and during summer (December to February) in southern Tasmania (Willcox et al. 2001, Lynch 2004, Sahlqvist 2007). Currently, most active jig vessels are based on the mainland where they can access the more reliable Bass Strait grounds, and only venture south to Tasmania when availability is particularly high. Although jig fishing occurs on several spatially (and temporally) discrete fishing grounds, this doesn't necessarily reflect any population structuring. Instead the location of jig fishing grounds has much to do with port locality and the presence of suitable jig ground (i.e. relatively flat and shallow sea floor). *Nototodarus gouldi* are also caught over much of southern Australia and year-round as a by-product by demersal trawl fisheries which operate on deep continental shelf and upper slope grounds, targeting more valuable finfish species (Lynch 2004, Sahlqvist 2007).

Catches of *N. gouldi* have fluctuated greatly from year to year in both the jig and trawl fisheries. Between 1995 and 2007 the Commonwealth managed jig fishery (SSJF) annual catches have fluctuated by a factor of almost 6- from 360 tonnes in 2000 to more than 2000 tonnes in 1997 (Sahlqvist 2007). In Tasmanian waters, jig catches have been even more sporadic, with low catches (0.8 - 12 tonnes) taken in most years, but large peaks occurred in 1999/00 (476 tonnes; Willcox et al. 2001) and more recently in 2006/07 (at least 690 tonnes; J. Lyle *pers. comm.*). Demersal trawl catch is slightly more stable than the jig catches, but has ranged from 315 to 1052 tonnes since 1986 (Sahlqvist 2007). The demersal trawl and jig fisheries do not appear to have any common trend in their annual catch trajectories.

Although the scale of the *N. gouldi* fisheries are small by global squid fishery standards, it is the most important commercially exploited cephalopod in Australia (in volume of catch), and has considerable potential for expansion, at least in terms of effort applied, with less than 30% of the allocated SSJF Statutory Fishing Rights assigned to active vessels in 2006 (J. Davis *pers comm.*).

THESIS STRUCTURE & PRESENTATION

The spatial and temporal variability evident in the availability of *N. gouldi* to commercial fisheries and higher predators in southern Australia prompts the questions: how does the abundance of *N. gouldi* vary in space and time, and what factors might be driving these patterns? This study approaches these questions within a hierarchical framework, investigating the ecology of *N. gouldi* at several spatial and temporal scales. Patterns of *N. gouldi* distribution and abundance are described and links to environmental conditions investigated, firstly over a broad spatial area, and then by focussing on inter-annual variability at a particularly productive location.

This thesis examines if large-scale spatial and seasonal patterns in abundance can be explained by environmental variability, and if annual abundance be predicted from pre-recruitment environmental conditions. Continuing investigations at a smaller spatial scale, this thesis then explores how population biology varies inter-annually and the relationship between population structure, life history characteristics and abundance- are changes in population biomass linked to the biological characteristics of the population? Finally, small-scale movement and activity patterns of *N. gouldi* are examined to provide insight into habitat utilisation and occupancy times in relation to the seasonal availability on an inshore jig ground.

There are four chapters in the body of this thesis, each briefly outlined below. Each chapter has been written as a free-standing research paper and can therefore be read independently without the need to refer back to other areas of the thesis for clarification. However, this has resulted in some repetition between the main chapters, particularly in the introductory sections.

Chapter 2:

Broad-scale spatio-temporal patterns of arrow squid (*Nototodarus gouldi*) abundance in southeastern Australia: investigation of environmental associations.

Little is known of the ecology of *N. gouldi,* so the first step was to describe spatial and seasonal patterns of distribution and abundance in southeastern Australia. Catch and effort data from a demersal trawl fishery were used to calculate the probability of *N. gouldi* (which is a non-targeted by-product) being present in a particular location at a particular time, and the relative abundance when present. Statistical models were used to determine if spatio-temporal patterns could be related to environmental variables. This chapter provided an important basis for the thesis and suggested the appropriate scale and scope for further work.

Chapter 3:

Inter-annual variability in arrow squid (*Nototodarus gouldi*) abundance in the Bonney upwelling, southern Australia: environmental correlations and predictive models.

This chapter builds on chapter 2, by examining inter-annual variability in abundance at one of the most productive locations for *N. gouldi* in southeastern Australia. The aim of this chapter was to investigate if predictive models of *N. gouldi* annual abundance could be developed using a suite of time-lagged environmental variables. As two different fisheries for *N. gouldi* operate in the area, there was the opportunity to compare indices of abundance derived from the two fisheries which generally operate at different depths, and consider the ecological implications of their relationship. This chapter provided important insight into the processes driving variability in available biomass and the potential application of predictive models for forecasting and managing squid fisheries.

Chapter 4:

Inter-annual variability in population structure and life history parameters of *Nototodarus gouldi* in southeastern Tasmania, Australia.

Changes in the available abundance of squid are often attributed to environmental influences and these can also impact on population structure and life history characteristics. This chapter examines inter-annual variability in the population biology of *N. gouldi* collected over 4 seasons (1999/00, 2000/01, 2002/03 and 2003/04) from the same location, and the relationship with annual available abundance which fluctuated greatly in the years sampled. Few studies have examined inter-annual variability in squid population structure and life history characteristics, although seasonal and latitudinal comparisons show that these parameters can vary greatly in response to environmental variability. This study also provides a description of the population biology of *N. gouldi* on an inshore jig fishing ground (in contrast to previous work from trawl caught squid) and discusses the possibility of ontogenetic migrations between jig grounds in shallow continental shelf waters and the trawl grounds in deeper shelf-break and upper slope waters.

Chapter 5:

Tracking arrow squid movements with an automated acoustic telemetry system: *Nototodarus gouldi* in inshore Tasmanian waters.

This study used an acoustic telemetry array to track *N. gouldi* movements and activity patterns in Storm Bay, southeastern Tasmania during the austral summer in 2002/03. The aim of this study was to gain insight into the behaviour of *N. gouldi* when in inshore aggregations, and in particular the movement dynamics of the population and the timing of emigration from the study area. This work contributes to understanding of the seasonal abundance of *N. gouldi* in inshore shelf waters.

Chapter 5 is presented as published:

Stark, K.E., G.D. Jackson, J.M. Lyle (2005). Tracking arrow squid movements with an automated acoustic telemetry system. *Marine Ecology Progress Series* 299: 167-177.

The relative contributions if each co-author are outlined in the Statement of co-authorship (page ii).

A brief overview of the general findings and conclusions of the thesis are provided in **Chapter 6**, along with a discussion of the implications of these findings to our understanding of squid population dynamics, and suggestions for future research.